

Marine boring bivalve mollusks from Isla Margarita, Venezuela

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ABSTRACT Marine endolithic and wood-boring bivalve mollusks living in rocks, corals, wood, and shells were surveyed on the Caribbean coast of Venezuela at Isla Margarita between 2004 and 2008. These surveys were supplemented with boring mollusk data from malacological collections in Venezuelan museums. A total of 571 individuals, corresponding to 3 orders, 4 families, 15 genera, and 20 species were identified and analyzed. The species with the widest distribution were: *Leiosolenus aristatus* which was found in 14 of the 24 localities, followed by *Leiosolenus bisulcatus* and *Choristodon robustus*, found in eight and six localities, respectively. The remaining species had low densities in the region, being collected in only one to four of the localities sampled. The total number of species reported here represents 68% of the boring mollusks that have been documented in Venezuelan coastal waters. This study represents the first work focused exclusively on the examination of the cryptofaunal mollusks of Isla Margarita, Venezuela.

KEY WORDS Shipworms, cryptofauna, Teredinidae, Pholadidae, Gastrochaenidae, Mytilidae, Petricolidae, Margarita Island, Isla Margarita Venezuela, boring bivalves, endolithic.

INTRODUCTION

Bivalve mollusks from a range of families have developed a peculiar lifestyle of boring into and living in hard substratum such as rocks, compacted sediments, woods, corals, and even other mollusk shells (Bagur *et al.*, 2013; Cognetti *et al.*, 2001; Valentich-Scott and Dinesen, 2004; Valentich-Scott and Tonkerd, 2008; Yonge, 1955). These boring bivalve mollusks can be classified into two artificial groups: the first including those that burrow into a substratum to utilize the unusual habitat, and the secondly species that use the substratum as a habitat and for nutrition (Ewald *et al.*, 1984).

The lithophagans (Mytilidae) are among the more recognized boring mollusks. They excavate calcareous rocks or corals using an acidic substance secreted by a gland located in the mantle margin (Morton and Scott, 1980; Bagur *et al.*, 2013; Kleeman, 1980; 1982; 1984; 1986). By contrast, the pholads (Pholadidae) physically bore into siltstone, shale, or coral with the roughened exterior of their valves (Cognetti *et al.*, 2001; Valentich-Scott and Dinesen, 2004; Valentich-Scott and Tonkerd, 2008). In addition, shipworms (Teredinidae), use their small anterior shells to bore into wood and other plant-based substrata (Turner, 1966;

Distel *et al.*, 2011). The shipworms constitute one of the main biological agents involved in the degradation of wood in the marine environment, contributing to its access in the food chain as a source of energy (Distel *et al.*, 2011). However, in coastal communities around the world, some of these bivalves are much maligned, as they inflict serious damage on wooden piers, culture systems, and boats (Nair and Dharmaraj, 1979; Sipe *et al.*, 2000; Velásquez *et al.*, 2011).

Only two reports have focused exclusively on the diversity of marine boring bivalve mollusks along the Venezuelan coast. Nair (1975) detailed the location of ten boring species from the family Teredinidae in the Golfo de Cariaco, and Ewald *et al.* (1984) reported 11 species of boring bivalves from the Lake Maracaibo Basin.

There are a few taxonomic reports that have included boring bivalves in Venezuelan coastal waters. Beauperthuy (1967) reported on the Mytilidae in Venezuela and mentioned three species of *Lithophaga*. Lodeiros *et al.* (1999) presented a taxonomic inventory of mollusks and listed six boring mollusk species for the northern coast of the country. Bitter and Martinez (2001) described three species from the coast of Falcón. Macsotay and Campos (2001) registered nine boring bivalve species on the northeast of Isla Margarita and Capelo *et al.* (2009) documented the presence of three species for the Golfo de Paria and Orinoco Delta.

Isla Margarita is one of the Minor or Southern Antilles located in Venezuela's northern region (González, 2007). It constitutes two islands connected by a sandbar and a mangrove lagoon of 30 km² length (Monente, 1978). Isla Margarita has one of the highest ecosystem and species diversities known in the Caribbean region. This is possibly due to its size (1.072

km²), proximity to the main land (22 km), and the heterogeneity of its landscapes (Sanz, 2007).

This study examines the distribution and composition of littoral endolithic bivalve mollusks on Isla Margarita, providing a foundation to expand our understanding of the biodiversity of this group in South America.

Abbreviations used in the text are:

MOBR-M, Museo Oceanológico Benigno Román, Colección de Moluscos, Isla Margarita, Venezuela;

MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; spec, specimens.

MATERIALS AND METHODS

Field surveys were performed between May 2004 and June 2008 along the coastline of Isla Margarita and Los Frailes archipelago (Figure 1; Table 1) within the littoral zones between 0.5 and 5 meters depth. Samples were collected manually using hand tools (hammer, hand saw, pliers) to break the substratum where the bivalves live (rocks, dead corals, mangrove roots, wood debris, gastropod and bivalve shells). In the sublittoral zone (coral reefs, mangrove roots, and other sunken structures) sampling was accomplished with the aid of snorkeling equipment. In some cases, when the extraction of the organism in the field was difficult, the substratum was transported to the laboratory in seawater containers.

In the laboratory, samples were separated and quantified. Substratum samples were dissected for the complete extraction of essential taxonomic structures of the endolithic bivalves (*e.g.* valves, and pallets of teredinids). After that, the valves of the mollusks were immersed in a solution of commercial chlorine (3%) for 12

hours or until all associated epibionts were dissolved.

These surveys were supplemented with boring mollusk data from the malacological collections of the Museum Hno, Benigno Román, La Salle Foundation, Isla de Margarita, Venezuela.

Taxa were identified to the lowest level possible using the taxonomic keys available in specialized literature. To confirm the identity *Teredinidae* comparisons were made with specimens in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA and the Santa Barbara Museum of Natural History, Santa Barbara, California, USA. Additionally, synonyms, global distribution and valid names of the species identified were obtained using Capelo and Buitrago (1998), Coan and Valentich-Scott (2012), Daccarett and Bossio (2011), Díaz and Puyana (1994), Ewald *et al.* (1984), Keen (1971), Lodeiros *et al.* (1999), Macsotay and Campos (2001), Mikkelsen and Bieler (2007), Monari (2009), Ríos, (2009), Tunnell *et al.* (2010), Turner (1966, 1971), and Valentich-Scott and Dinesen (2004). All samples were preserved in 70% ethyl alcohol. Voucher specimens were deposited in Oceanologic Museum Hno., Benigno Román, at the Marine Investigation Station of Margarita located in the La Salle Foundation (MOBR-M).

For most families, specimen measurements correspond to the length of the valves, whereas measurements of specimens in the *Teredinidae* correspond to the pallet length. In both cases, values were expressed as mean and standard deviations ($X \pm SD$).

RESULTS

We collected and analyzed a total of 571 specimens of marine endolithic bivalve

mollusks, distributed in 3 orders, 4 families, 15 genera, and 20 species. Of the total, 41.8% were members of the *Mytilidae*, 35.1% *Pholadidae*, 15.61% *Veneridae*, 4.38% *Teredinidae*, and 3.16% *Gastrochaenidae*. We have also made a list of previous reports of marine boring mollusks reported from Venezuelan coastal waters and their sampling locations (Table 2).

Systematic Account

Phylum Mollusca

Class Bivalvia

Order Mytiloida

Family Mytilidae (Rafinesque, 1815)

Leiosolenus aristatus (Dillwyn, 1817)
(Figure 2)

Mytilus aristatus Dillwyn, 1817; *Modiola caudigera* Lamarck, 1819; *Lithophagus caudatus* (Gray, 1826); *Mytilus ropan* Deshayes, in Lamarck and Deshayes, 1836; *Lithophagus aristatus* var. *gracilior* (Carpenter, 1857); *Lithophagus aristatus* var. *tumidior* (Carpenter, 1857); *Dactylus carpenteri* Mörch, 1861; *Lithodomus forficatus* Ravenel, 1861; *Modiola excavata* de Folin, 1867; *Lithodomus bipenniferus* Guppy, 1877.

Diagnosis: Shell elongate, inflated, cylindrical; beaks subterminal; periostracum yellow-brown; valves mostly covered by calcareous incrustations; characterized by elongated pointed incrustations at the posterior end, forming overlapping scissor-like forceps.

Material Examined: Playa El Tirano: 9 May 2004. 6 spec. Average length: 20 mm $\pm$ 2.4 (MOBR-M-3188). Playa Puerto Cruz: 16 May 2004. 9 spec. Average length: 22.6 mm $\pm$ 3.6 (MOBR-M-3189). Playa Parguito: 9 March 2004. 10 spec. Average length: 14.8 mm $\pm$ 2.7 (MOBR-M-3190). Playa Zaragoza: 9 March

2004. 5 spec. Average length: 28.2 mm $\pm$ 4.1 (MOBR-M-3191). Chacachacare: 3 May 2003. 1 spec. Length: 27.2 mm (MOBR-M-3192). Archipelago Los Frailes, La Pecha: 30 May 2006. 2 spec. Average length: 3.1 mm $\pm$ 5.4 (MOBR-M-3395). Pampatar, Pta Ballena: 7 May 2003. 8 spec. Average length: 21.2 mm $\pm$ 3.7 (MOBR-M-3532). Juan Griego, Playa La Galera: 20 June 2007. 1 spec. Length: 15 mm (MOBR-M-3698). Playa Zaragoza: 12 July 2008. 17 spec. Average length: 20.6 mm $\pm$ 3.2 (MOBR-M-3916). Taguantar: July 2008. 1 spec. Length: 23.2 mm $\pm$ 2.2 (MOBR-M-3918). Playa El Tunal: 18 July 2008. 4 spec. Average length: 10.9 mm $\pm$ 0.9 (MOBR-M-3924).

Habitat: Commonly found boring into corals, coral fragments, and mollusk shells in shallow waters (Coan and Valentich-Scott, 2012; Díaz and Puyana, 1994; Valentich-Scott and Dinesen, 2004). Bullock and Boss (1971) and Alvarez-Cerillo *et al.* (2017) reported the occurrence of *L. aristatus* boring into chitons shell plates.

Distribution: Western Atlantic: North Carolina to Texas, USA, throughout the Caribbean, in South America from Colombia to southern Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010). Also found in the eastern Atlantic Ocean and Mediterranean Sea (Díaz and Puyana, 1994), and the eastern Pacific Ocean (Coan and Valentich-Scott, 2012).

Remarks: Mikkelsen and Bieler (2007) invoked ICZN Article 23.9, Reversal of Precedence, to maintain the usage of the prevailing d'Orbigny names, *Leiosolenus aristatus*, *Leiosolenus bisulcatus*, and *Lithophaga antillarum*, over the earlier Philippi names. Bieler (2010) subsequently reported that Article 23.9.1.2 (name not used after 1899) was not met. However, Article 23.10, the Erroneous Reversal of Precedence, stipulates that the

prevailing usages must be maintained until the ICZN Commission makes a ruling. Currently no cases on this issue are in front of the Commission and we must follow the prevailing usage, contrary to Kleemann (2009).

Leiosolenus bisulcatus (d'Orbigny, 1853)
(Figure 3)

Lithodomus bisulcata d'Orbigny, 1853, *nomen protectum*; *Modiola appendiculata* Philippi, 1846; *Lithodomus biexcavatus* Reeve, 1857.

Diagnosis: Shell elongate, cylindrical, with flare along the posterodorsal margin; sharp, oblique, indented line dividing each valve into two sections; shell covered with a thick feathery calcareous incrustations, thicker posteriorly and ventrally.

Material Examined: Punta de Piedras, El Atolladar: 25 April 2003. 5 spec. Average length: 23 mm $\pm$ 6.3 (MOBR-M-3184). Punta de Piedras, Laguna Pta de Piedras: 14 April 2003. 2 spec. Average length: 32.6 mm $\pm$ 8.6 (MOBR-M-3185). Punta de Piedras, Laguna Pta de Piedras: 14 April 2003. 1 spec. Length: 36 mm (MOBR-M-3186). Playa Zaragoza: 9 May 2004. 1 spec. Length: 34.6 mm (MOBR-M-3187). Playa Zaragoza: 12 July 2008. 1 spec. Length: 31.2 mm (MOBR-M-3917). Playa El Tunal: 12 July 2008. 1 spec. Length: 26.8 mm (MOBR-M-3919). Playa El Tunal: 18 July 2008. 1 spec. Length: 14.5 mm (MOBR-M-3923).

Habitat: Found boring in rocks, conglomerate, and live and dead corals (Kleemann, 2009). This species can also be found boring into living mollusk shells, such as *Strombus*, and in calcareous rocks (Turner and Boss, 1962; Valentich-Scott and Dinesen, 2004).

Distribution: Western Atlantic from North Carolina to Texas, USA, throughout the

Caribbean, in South America from Colombia to southern Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010).

Lithophaga antillarum (d'Orbigny, 1853)
(Figure 4)

Lithodomus antillarum d'Orbigny, 1853, *nomen protecum*; *Modiola corrugata* Philippi, 1846; *Modiola ferruginea* Philippi, 1847; *Lithophagus caperatus* Philippi, 1849; *Lithophaga straminea* Dunker, 1880.

Diagnosis: Shell elongate, cylindrical, fragile; beaks subterminal, but not extending past anterior end; periostracum light to medium brown, dehiscent; sculpture of fine vertical lines over most of shell, and heavy commarginal undulations posterodorsally; without calcareous incrustations on exterior of shell.

Material Examined: El Guamache, Varadero: 1 May 2003. 1 spec. Length: 43.5 mm (MOBR-M-3171).

Habitat: Commonly found from the subtidal to 30 meters, boring into dead coral and limestone (Beaperthuy, 1967; Díaz and Puyana, 1994; Valentich-Scott and Dinesen, 2004).

Distribution: Western Atlantic from southern Florida and throughout the Caribbean, in South America from Colombia to the northeast of Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Rios, 2009; Valentich-Scott and Dinesen, 2004).

Gregariella coralliophaga (Gmelin, 1791)
(Figure 5)

Mytilus coralliophaga Gmelin, 1791; *Modiola semen* Lamarck, 1819; *Modiola divaricata* Philippi, 1847; *Lithodomus argentea* Reeve,

1858; *Lithodomus gossei* Reeve, 1858; *Tibialectus otteri* Iredale, 1939.

Diagnosis: Shell ovate; beaks subterminal, but not extending past anterior end; periostracum reddish-brown; ventral margin finely serrate; dorsal margin with posterior crest from which curved striae radiate posteriorly and ventrally; hinge weak; inner dorsal margin finely denticulate; shell interior highly iridescent; without calcareous incrustations on exterior of shell, but frequently densely hirsute.

Material Examined: Pampatar: collection date unknown. Length: 3.2 mm (MOBR-M-0157).

Habitat: Found boring into calcareous stones in shallow waters (Díaz and Puyana, 1994) and reported boring into limestone (Romero *et al.*, 2003).

Distribution: Western Atlantic from North Carolina to Texas, USA, in South America from Colombia to southern Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010). Also distributed in the Indo-West Pacific (Printrakoon *et al.*, 2016). Records from the eastern Pacific are in error (Coan and Valentich-Scott, 2012).

Order Veneroida

Family Petricolidae d'Orbigny, 1840

Choristodon robustus (Sowerby I, 1834)
(Figure 6)

Petricola robusta G. B. Sowerby I, 1834; *Rupellaria typica* Jonas, 1844; *Petricola robusta* Philippi, 1849; *Petricola sinuosa* Conrad, 1849; *Petricola bulbosa* Gould, 1851; *Petricola anachoreta* de Folin, 1867; *Petricola venusta* de Folin, 1867; *Petricola buwaldi* B. L. Clark, 1915; *Petricola riocanensis* Maury, 1917.

Diagnosis: Shell grayish white; broadly rounded anteriorly; produced posteriorly, moderately inflated; inequilateral, posterior end longer; sculpture of strong, narrow, irregularly spaced radial ribs crossed by commarginal ribs, giving a beaded appearance at intersections; pallial sinus deep, broad.

Material Examined: El Maguey. 17 May 2003. 5 spec. Average length: 17 mm $\pm$ 2.7 (MOBR-M-3178). Pampatar, Pta Ballena: 7 May 2003. 5 spec. Average length: 16 mm $\pm$ 6.1 (MOBR-M-3179). Pampatar, Pta Ballena: 7 May 2003. 1 spec. Length: 30.5 mm (MOBR-M-3180). Punta de Piedras, Muelle FLASA: 9 May 2003. 4 spec. Average length: 18.1 mm $\pm$ 0.6 (MOBR-M-3181). Archipelago Los Frailes, La Pecha: 30 May 2006. 1 spec. Length: 17.8 mm (MOBR-M-3401). Pampatar, Pta Ballena: 7 May 2003. 1 spec. Length: 16.8 mm (MOBR-M-3531). Playa Guacuco: August 2004. 1 spec. Length: 11.4 mm (MOBR-M-3540). Playa El Tunal: 18 June. 5 spec. Average length: 14.9 mm $\pm$ 3.8 (MOBR-M-3926).

Habitat: Found in calcareous substrata, such as bivalve shells, colonial corals, and calcareous bryozoans, also found in polychaete tubes made of agglutinated sand (Coan and Valentich-Scott, 2012).

Distribution: Western Atlantic from North Carolina to Texas, USA, in South America from Colombia to southern Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010). Also in the eastern Pacific from Laguna Ojo de Liebre on the outer coast of Baja California, Mexico, to Piura, Peru (Coan and Valentich-Scott, 2012).

Family Pholadidae (Lamarck, 1809)

Martesia cuneiformis (Say, 1822)
(Figures 7, 8)

Pholas cuneiformis Say, 1822; *Pholas caribaea* d'Orbigny, 1846; *Pholas falcata* G. B. Sowerby II, 1872 (*non* W. Wood, 1815); *Pholas krebsi* Krebs, 1864.

Diagnosis: Shell ovate, broader anteriorly, narrower posteriorly; mesoplax (accessory calcareous plate on top of umbones) thick, ovate to wedge-shaped, centrally grooved, commarginally sculptured; valves divided into sections by a narrow radial sulcus extending from beaks to ventral margin; sculpture anteriorly of strongly imbricate commarginal ribs, posteriorly with broad, rounded, widely-spaced commarginal ribs.

Material Examined: Porlamar, Laguna El Morro: 15 July 2008. 2 spec. Average length: 3.1 mm $\pm$ 1.1 (MOBR-M-3977).

Habitat: Found boring into mangrove roots and drift wood (Tunnell *et al.*, 2010).

Distribution: Western Atlantic from North Carolina to Texas, USA, in South America from Colombia to northern Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Tunnell *et al.*, 2010). Also in the eastern Pacific Ocean from California, USA, to Panama (Coan and Valentich-Scott, 2012).

Martesia fragilis Verrill and Bush, 1898
(Figures 9, 10)

Martesia (*Martesiella*) *fragilis* Verrill and Bush, 1898; *Pholadidea* (*Penitella*) *minuscule* Dall, 1908; *Martesia bahamensis* (Bartsch and Rehder, 1945); *Martesia* (*Diplopax*) *exquisita*

Bartsch and Rehder, 1945; *Martesia (Diploplax) bahamensis* Bartsch and Rehder, 1945.

Material Examined: Boca de Pozo: 20 April 2008. 9 spec. Average length: 6.2 mm $\pm$ 0.1 (MOBR-M-3934).

Diagnosis: Shell subovate, short; mesoplax ovate-elongate with peripheral keel and commarginal sculpture; valves divided into sections by moderate radial sulcus extending from beaks to ventral margin; sculpture anteriorly of weakly imbricate commarginal ribs, posteriorly with narrow, widely-spaced commarginal ribs.

Habitat: Found boring in wood or mangrove roots (Díaz and Puyana, 1994).

Distribution: Western Atlantic from North Carolina, USA to Uruguay (Díaz and Puyana, 1994). Eastern Pacific from Mexico to Panama (Díaz and Puyana, 1994).

Martesia striata (Linnaeus, 1758)
(Figure 11)

Pholas striata Linnaeus, 1758; *Pholas pusillis* Linnaeus, 1758; for extended synonymy list see Turner (1966).

Diagnosis: Shell variable in shape but usually long and pear-shaped (juveniles nearly circular), moderately fragile; mesoplax subcircular, without central groove, with irregular wrinkles but no commarginal sculpture; anterior end with closely spaced, imbricate commarginal ribs; posterior slope with wide, low commarginal ribs and undulations.

Material Examined: Punta de Piedras, Punta de Piedras lagoon: 1 April 1992. 7 spec. Average length: 20.7 mm $\pm$ 6.1 (MOBR-M-1238). El Guamache, El Oasis: 1 May 2003. 5

spec. Average length: 19.3 $\pm$ 2.2 (MOBR-M-3136). Punta de Piedras, El Atolladar: 25 April 2003. 1 spec. Length: 15.6 mm (MOBR-M-3182). El Guamache, El Oasis: 1 May 2003. 2 spec. Average length: 22.6 mm $\pm$ 2.5 (MOBR-M-3183). Punta de Piedras, Laguna de Pta de Piedras: 25 April 2003. 9 spec. Average length: 19.7 mm $\pm$ 4.1 (MOBR-M-3193). El Guamache: 25 April 2003. 4 spec. Average length: 20.8 mm $\pm$ 1.4 (MOBR-M-3194). Punta de Piedras, Laguna de Pta de Piedras: 17 April 2003. 15 spec. Average length: 16.1 mm $\pm$ 5.2 (MOBR-M-3195). El Guamache, El Oasis: 1 May 2003. 3 spec. Average length: 23.8 mm $\pm$ 2.3 (MOBR-M-3197). La Isleta, Las Marites lagoon: 15 July 2008. 6 spec. Average length: 21.8 mm $\pm$ 4.3 (MOBR-M-3920). Porlamar, El Morro lagoon: 15 June 2008. 2 spec. Average length: 8.7 mm $\pm$ 7.8 (MOBR-M-3922). Playa El Tunal: 18 June 2008. 2 spec. Average length: 3.6 mm $\pm$ 0.04 (MOBR-M-3925).

Habitat: Found boring in living wood or fallen sunken wood of the red mangrove *Rhizophora mangle*. We also collected specimens boring into wood boats and dock pilings. This species has been found boring in PVC pipe and pieces of bamboo (Scott, 1991).

Distribution: Western Atlantic: North Carolina to Texas, USA, throughout the Caribbean; in South America from Colombia to southern Brazil (Daccarett and Bossio, 2011; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010). Also in tropical waters of the eastern Pacific and Indo-Pacific (Coan and Valentich-Scott, 2012).

Barnea truncata (Say, 1822)
(Figures 12, 13)

Pholas truncata Say, 1822

Diagnosis: Shell cylindrical, fragile, white; anterior end pointed; posterior end subtruncate; sculpture of widely spaced radial ribs overlain by closely spaced imbricated commarginal ribs on anterior end and medial section; radial sculpture absent posterodorsally.

Material Examined: Playa La Restinga, El Saco: 17 April 2003. 1 spec. Length: 44.5 mm (MOBR-M-3177). Punta de Piedras, El Atolladar: 15 December 2008. 1 spec. Length: 48.7 mm (MOBR-M-3792).

Habitat: Found boring in wood, clay, and soft rocks (Calvalho, 1994; Díaz and Puyana, 1994), and also boring into live and dead corals (Monari, 2009).

Distribution: Western Atlantic from Massachusetts to Texas, USA, in South America from Colombia, Venezuela, and Brazil (Calvalho, 1994; Daccarett and Bossio, 2011; Humfrey, 1975; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010) In the eastern Atlantic: Senegal (Abbott, 1974; Calvalho, 1994) and Angola (Díaz and Puyana, 1994), and in the Western Pacific: Gold Coast, Australia (Abbott, 1974).

Cyrtopleura costata (Linnaeus, 1758)
(Figures 14, 15)

Pholas costata Linnaeus, 1758; *Leuconyx tayleriana* H. Adams and A. Adams, 1863; *Capulus shreevei* Conrad, 1869.

Diagnosis: Shell ovate-elongate, fragile, chalky-white; sculpture of strong radial ribs over most exterior surfaces, more widely spaced

and imbricate anteriorly, and fine commarginal ribs and striae; umbonal reflection well-separated from dorsal surface; valves widely gaping, touching only dorsally.

Material Examined: La Restinga: 1 January 1970. 2 spec. Average length: 59.5 mm $\pm$ 1.2 (MOBR-M-1067).

Habitat: Usually found buried in mud flats (Warmke and Abbott, 1961) or boring soft rocks (Calvalho, 1994).

Distribution: Mainly found in the western Atlantic from Cape Cod, Massachusetts to Texas, USA, in South America from Surinam to southern Brazil (Calvalho, 1994; Clench, 1973; Humfrey, 1975; Mikkelsen and Bieler, 2007; Rios, 2009; Tunnell *et al.*, 2010).

Pholas campechiensis Gmelin, 1791
(Figures 16, 17)

Pholas campechiensis Gmelin, 1791; *Pholas oblongata* Say, 1822; *Pholas candeana* d'Orbigny, 1853.

Diagnosis: Shell ovate-cylindrical, fragile, chalky white; sculpture of imbricate, evenly spaced radial ribs, greatly reduced posteriorly, and fine commarginal ribs and striae; umbonal reflection separated from dorsal surface; valves slightly gaping at anterior and posterior end.

Material examined: La Restinga, Playa El Saco: 15 May 2003. 2 spec. Average length: 85.2 mm $\pm$ 14.5 (MOBR-M-3176). Porlamar, Playa Concorde: 15 July 2008. 1 spec. Length: 27.8 mm (MOBR-M-3921).

Habitat: Found deeply burrowing into compacted clay, wood, or soft rocks (Díaz and Puyana, 1994; Rios, 2009).

Distribution: West Atlantic from North Carolina to Texas, USA and throughout the Caribbean, in South America from Colombia, Venezuela, Surinam, Brazil and Uruguay (Calvalho, 1994; Daccarett and Bossio, 2011; Díaz and Puyana, 1994; Rios, 2009; Tunnell *et al.*, 2010). Also in the eastern Atlantic between Senegal and Liberia (Díaz and Puyana, 1994).

Family Teredinidae (Rafinesque, 1815)

Bankia destructa Clench and Turner, 1946
(Figures 18-19)

Diagnosis: Pallets elongated with separated cup-shaped segments; periostracal ridge of the segments serrated; inner and outer margins of the segments serrated; serrations on outer face fine, on inner longer and coarser; segments with short serrated awns; siphons separated.

Material Examined: Punta de Piedras, Laguna de Pta de Piedras: 20 August 2007. 1 spec. Length: 2.8 mm (MOBR-M-3936). Punta de Piedras, Laguna de Pta de Piedras: 20 August 2007. 1 spec. Length: 3.4 mm (MOBR-M-3937). Punta de Piedras, Laguna de Pta de Piedras : 20 August 2007. 1 spec. Length: 3 mm (MOBR-M-3938). Punta de Piedras, Laguna de Pta de Piedras: 15 July 2008. 1 spec. Length: 2.7 mm (MOBR-M-3981). Punta de Piedras, Laguna de Pta de Piedras: 11 October 2007. 1 spec. Length: 4.3 mm (MOBR-M-3982).

Comparative material: Canal Zone, Isla Naos, Panama. 17 April 1972. 10 spec (MCZ-351536).

Habitat: Found boring in wood (Abbott, 1974), especially mangrove roots and dock pilings (Díaz and Puyana, 1994).

Distribution: Western Atlantic: Florida to Central America; Gulf of Mexico and the

Caribbean Sea, Brazil (Abbott, 1974). In the eastern Pacific from Sinaloa, Mexico, to Guayas, Ecuador (Coan and Valentich-Scott, 2012).

Bankia gouldi (Bartsch, 1908)
(Figure 20, 21)

Xylotrya gouldi Bartsch, 1908; *Bankia mexicana* Bartsch, 1921; *Bankia schrencki* Moll, 1935.

Diagnosis: Pallets composed of numerous segments on a long stalk, segments cone-shaped without serrations on the margins; cones broadly triangular, with smooth, drawn-out edges, lateral margins extended into fine short awns; periostracal margin on the inner face forming web connecting awns; narrow periostracal margin of outer face with short longitudinal striations.

Material Examined: Punta de Piedras, Laguna de Pta de Piedras: 20 November 2007. 1 spec. Length: 4.4 mm (MOBR-M-3939).

Comparative Material: Santa Marta, Colombia. 2 February 1936. 1 spec (MCZ-122502). Santa Marta, Colombia. 2 February 1936. 1 spec (MCZ-122526). Santa Marta, Colombia: 2 February 1936. 1 spec (MCZ-122542). Santa Marta, Colombia: 2 February 1936. 1 spec (MCZ-122499).

Habitat: Commonly found in any type of sunken wood (Díaz and Puyana, 1994).

Distribution: Western Atlantic: New Jersey to Texas, USA, in South America from Colombia to Uruguay (Tunnell *et al.*, 2010; Daccarett and Bossio, 2011; Rios, 2009). In the eastern Pacific from Sinaloa, Mexico, to Guayas, Ecuador (Coan and Valentich-Scott, 2012).

Bankia carinata (J. E. Gray, 1827)
(Figures 22, 23)

Teredo carinata J.E. Gray, 1827; *Teredo stutchburyi* Blainville, 1828; *Xylotrya philippi* Gray, 1851; *Bankia bipalmata* Delle Chiaje, 1929; *Bankia caribbea* Clench and Turner, 1929; *Bankia kamiyai* Roch, 1929; *Bankia orientalis* Roch, 1929; *Bankia indica* Nair, 1954; *Bankia edmondsdoni* Nair, 1956.

Diagnosis: Pallets not serrated on margin cones; funnel-shaped cones moderately spaced; periostracal horns short and wide, projecting outwardly away from upper segment; embryonic segments stacked in a compact plate-shaped end; periostracal margin on inner and outer faces about equal.

Material Examined: Punta de Piedras, Laguna de Pta de Piedras : 11 October 2007. 1 spec. Length: 3.4 mm (MOBR-M-3983).

Comparative Material: Massachusetts, United States. 15 July 1983. 5 spec (MCZ- 351686). Massachusetts, United States. 15 July 1983. 2 spec (MCZ- 351688).

Habitat: Commonly found in boring wood or mangrove roots (Díaz and Puyana, 1994).

Distribution: Western Atlantic from the Gulf of Mexico, Caribbean Sea and Brazil (Abbott, 1974; Mikkelsen and Bieler, 2007; Díaz and Puyana, 1994). In the eastern Pacific from California, USA, to Guayas, Ecuador (Coan and Valentich-Scott, 2012). Also in the Mediterranean Sea (Díaz and Puyana, 1994), Africa; India, and Indian Ocean Islands (Abbott, 1974).

Lyrodus pedicellatus (de Quatrefages, 1849)
(Figures 24, 25)

Teredo pedicellata Quatrefages, 1849; *Teredo pedicellata* var. *truncata* Jeffreys, 1865; *Teredo chlorotica* Gould, 1870; and many other synonyms in various parts of the world (complete synonymy: R. D. Turner, 1966: 70-71).

Diagnosis: Shell with numerous, closely set ridges; pallet blade oval, calcareous, base covered partially by a brown-black horny periostracal cap, without deep furrow on outer face, frequently deeply excavated at the tip.

Material Examined: La Isleta, Las Marites lagoon: 15 July 2008. 1 spec. Length: 1.5 mm (MOBR-M-3929). La Isleta, Las Marites lagoon: 15 July 2008. 5 spec. Length: 2 mm (MOBR-M-3978).

Comparative Material: Puerto Cabello, Venezuela: 1 January 1938. 1 spec (MCZ- 123328). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123331). Puerto Cabello, Venezuela: 1 January 1938. 1 spec (MCZ- 123355). Puerto Cabello, Venezuela: [Date unknown]. 1 spec. (MCZ- 123483). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123519).

Distribution: Cosmopolitan in tropical and temperate waters around the world (Coan and Valentich-Scott, 2012; Mikkelsen and Bieler, 2007).

Habitat: Commonly found in any sunken wood (Díaz and Puyana, 1994).

Spathoteredo spatha (Jeffreys, 1860)
(Figures 26, 27)

Teredo spatha Jeffreys, 1860; *Teredo molli* Roch, 1931.

Diagnosis: Pallets obscurely segmented having a ribbed appearance; blade broadly oval in outline with a brownish periostracum around its base and a papillose encrustation distally.

Material Examined: Punta de Piedras, Laguna de Pta de Piedras: 11 October 2007. 1 spec. Length: 1.5 mm (MOBR-M-3983).

Comparative Material: Santa Marta, Chengue, Colombia. 20 August 1967. 15 spec (MCZ-278056).

Distribution: Caribbean Sea (Velásquez and López, 2015).

Habitat: Found boring in roots of the red mangrove *Rhizophora mangle* (Velásquez and López, 2015).

Remarks: The previous report of this species in Isla Margarita was made by Velásquez and López (2015). This species is originally described from Guernsey, England, from specimens collected from driftwood (Turner, 1966). It is not considered to be an established species in the region because all the specimens were found either in driftwood carried mainly by the Gulf Stream (Borges *et al.*, 2014; Velásquez and López, 2015).

Teredo furcifera von Martens, 1894
(Figure 28, 29)

Teredo furcifera (von Martens, 1894); *Teredo parksi* Bartsch, 1921; *Teredo furcillatus* Miller, 1924; *Teredo australasiatica* Roch, 1935; *Teredo furcata* Moll, 1935; *Teredo krappei*

Moll, 1935; *Teredo laciniata* Roch, 1935; *Teredo bensoni* Edmondsdon, 1946; *Teredo parksi madrasensis* Nair, 1958, *non* Nair, 1956.

Diagnosis: Palettes small, variable in shape, elongate to oval, usually concave; inside distal margin straight, rounded, V-shaped or U-shaped; periostracum covers the distal half of the blade but does not extend beyond the calcareous portion.

Material Examined: La Isleta, Las Marites lagoon: 15 July 2008. 1 spec. Length: 1.3 mm (MOBR-M-3930). La Isleta, Las Marites lagoon: 15 July 2008. 1 spec. Length: 1.4 mm (MOBR-M-3931). La Isleta, Las Marites lagoon: 15 July 2008. 1 spec. Length: 1.2 mm (MOBR-M-3932). Porlamar, El Morro lagoon: 15 July 2008. 7 spec. Average length: 1.8 mm $\pm$ 0.9 (MOBR-M-3979). Porlamar, El Morro lagoon: 15 July 2008. 1 spec. Length: 1.5mm (MOBR-M-3980).

Comparative Material: Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ-123454). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123457). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123459). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123461). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123462). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123464). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123466). Puerto Cabello, Venezuela: [Date unknown]. 1 spec (MCZ- 123467).

Habitat: Found boring into the roots of the red mangrove *Avicennia* sp. (Nair, 1975).

Distribution: Western Atlantic: Brazil (Rios, 2009). Also in the western Pacific, Malaysia (Singh and Sasekumar, 1994), Australia (Brearley *et al.*, 2003), and New Guinea (Rayner, 1979); in the central Pacific, Hawaii

(Turner, 1966), Colombia (Cantera, 2010), and Ecuador (Coan and Valentich-Scott, 2012); and in the Indian Ocean (Turner, 1966); Caribbean Sea, Venezuela (Nair 1975).

Family Gastrochaenidae (Gray, 1840)

Gastrochaena ovata Sowerby, 1834
(Figure 30)

Gastrochaena ovata G. B. Sowerby I, 1834.

Diagnosis: Shell ovate-elongate; beaks well behind anterior end; anterior end pointed; posterior end broadly rounded; sculpture of commarginal ribs and striae; ventral margin widely gaping.

Material Examined: Playa El Tunal: 18 June 2008. 1 spec. Length: 10 mm (MOBR-M-3928).

Habitat: Found boring in *Porites* corals or thick bivalve shells (Coan and Valentich-Scott, 2012).

Distribution: Throughout the tropical western Atlantic (Coan and Valentich-Scott, 2012); in South America from Colombia, and northern Brazil (Daccarett and Bossio, 2011; Díaz and Puyana, 1994; Mikkelsen and Bieler, 2007; Rios, 2009). In the eastern Pacific from Baja California, Mexico, to Guayas, Ecuador (Coan and Valentich-Scott, 2012).

Lamychaena hians (Gmelin, 1791)
(Figure 31)

Pholas hians Gmelin, 1791.

Diagnosis: Shell ovate-elongate; beaks terminal or subterminal; anterior end narrowly rounded, slightly produced ventrally in some; posterior end broadly rounded; sculpture of commarginal ribs and striae; ventral margin widely gaping.

Material Examined: Boca Chica: 6 March 2004. 2 spec. Average length: 9.9 ± 3.7 mm (MOBR-M-3172). Punta de Piedras: 17 April 2003. 3 spec. Average length: 10 ± 1.2 mm (MOBR-M-3173). Punta de Piedras: 17 April 2003. 2 spec. Average length: 10.7 ± 1.3 mm (MOBR-M-3174). Punta de Piedras, El Atolladar: 25 April 2003. 4 spec. Average length: 11.5 ± 0.6 mm. (MOBR-M-3175). Playa El Tunal: 25 April 2003. 4 spec. Average length: 4.2 ± 2.1 mm (MOBR-M-3927).

Habitat: Boring into living and dead corals, limestone, and into mollusk shells (Díaz and Puyana, 1994; Valentich-Scott and Dinesen, 2004).

Distribution: West Atlantic from North Carolina to Texas, USA, Bermuda, and West Indies; in South America from Colombia to Brazil (Daccarett and Bossio, 2011; Díaz and Puyana, 1994; Rios, 2009; Tunnell *et al.*, 2010).

Spengleria rostrata (Spengler, 1793)
(Figure 32)

Chaena rostrata Spengler, 1783; *Gastrochaena callosa* Philippi, 1845; *Gastrochaena chemnitziana* d'Orbigny, 1853.

Diagnosis: Shell quadrate-elongate; beaks well behind anterior end; anterior narrowly rounded; posterior end subtruncate; sculpture of commarginal ribs, very elevated from the umbones to the posterior margin; ventral margin widely gaping.

Material Examined: Los Frailes Archipelago, Punta Cachipo: 21 April 2005. 1 spec. Length: 27.7 mm (MOBR-M-3170).

Habitat: Boring into corals (Rios, 2009).

Distribution: Western Atlantic from North Carolina to southern Florida, USA, and in the West Indies; in South America from Colombia to southern Brazil (Daccarett and Bossio, 2011; Díaz and Puyana, 1994; Mikkelsen and Bieler, 2007; Rios, 2009).

DISCUSSION

Twenty endolithic bivalve mollusk species are here reported, which represents 68% of the taxa previously reported for the Venezuelan coast (Tables 1, 2). The boring mollusks with the widest distribution on Isla Margarita include *Leiosolenus aristatus* found at 14 of 24 sampling localities, followed by *Leiosolenus bisulcatus* and *Choristodon robustus* in eight and six localities, respectively. The endolithic bivalves sampled in this study were found mainly in rock, mollusk shells, and live or dead corals.

The endolithic bivalve fauna of Isla Margarita is much more speciose than that reported in the Florida Keys, but is less speciose compared with Indo-Pacific regions with high coral diversity. Valentich-Scott and Dinesen (2004) reported eight endolithic bivalves from limestone and dead corals in the Florida Keys, USA. In the Indo-Pacific Ocean, 21 coral boring species were sampled in the Kungkrabaen Bay region of Thailand (Valentich-Scott and Tongkerd, 2008) and 18 species from Ko Chang, Thailand (Printrakoon *et al.*, 2016). All three of these studies only examined corals or limestone habitats, and did not include wood or shell endoliths. We would expect the number of boring bivalve species to greatly increase in those regions if wood or shell substrata were examined. Additional studies on endolithic bivalves are needed in the tropical West Atlantic, especially those associated with live and dead corals, to more accurately compare with other geographic provinces.

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Table 1. Sampling sites and geographical coordinates.

Nº	Localities	Coordinates	
1	Punta de Piedras	10°54' N	64°6' W
2	El Guamache	10°52' N	64°3' W
3	Punta de Mangle	10°52' N	64°2' W
4	El Yaque	10°53' N	64°57' W
5	La Isleta	10°53' N	64°56' W
6	Porlamar	10°57' N	64°49' W
7	Pampatar	10°59' N	63°46' W
8	Guacuco beach	11°3' N	63°49' W
9	El Tirano	11°7' N	63°50' W
10	Parguito beach	11°7' N	63°50' W
11	Manzanillo	11°9' N	63°53' W
12	Puerto Cruz	11°7' N	63°55' W
13	Zaragoza	11°7' N	63°55' W
14	Juan Griego	11°5' N	63°58' W
15	Taguantar	11°4' N	64°0' W
16	La Restinga	10°59' N	64°7' W
17	El Saco	11°3' N	64°12' W
18	El Maguey	11°4' N	64°11' W
19	El Tunal	11°4' N	64°17' W
20	Boca de Pozo	11°0' N	64°22' W
21	Boca Chica	10°57' N	64°21' W
22	Boca de Río	10°58' N	64°10' W
23	Chacachacare	10°57' N	64°9' W
24	Los Frailes	11°11' N	63°44' W

List of references cited in the Table 2: 1 = Clench and Turner, 1946; 2 = Turner and Brown, 1953; 3 = Turner, 1955; 4 = Turner, 1966; 5 = Beuperthuy, 1967; 6 = Princz, 1973; 7 = Nair, 1975; 8 = Princz *et al.* 1981; 9 = Ewald *et al.* 1984; 10 = Buitrago and Capelo, 1993; 11 = Carvajal and Capelo, 1993; 12 = Ramos and Robaina, 1994; 13 = Buitrago, Capelo and Gutiérrez, 1996; 14 = Leon, 1997; 15 = Capelo and Buitrago, 1998; 16 = Bitter and Martinez, 2001; 17 = Macsotay and Campos, 2001; 18 = Romero *et al.* 2003; 19 = Perez *et al.* 2007; 20 = Capelo *et al.* 2009; 21 = Lasso *et al.* 2009; 22 = Velásquez and López 2015; 23 = Velásquez and López 2016.

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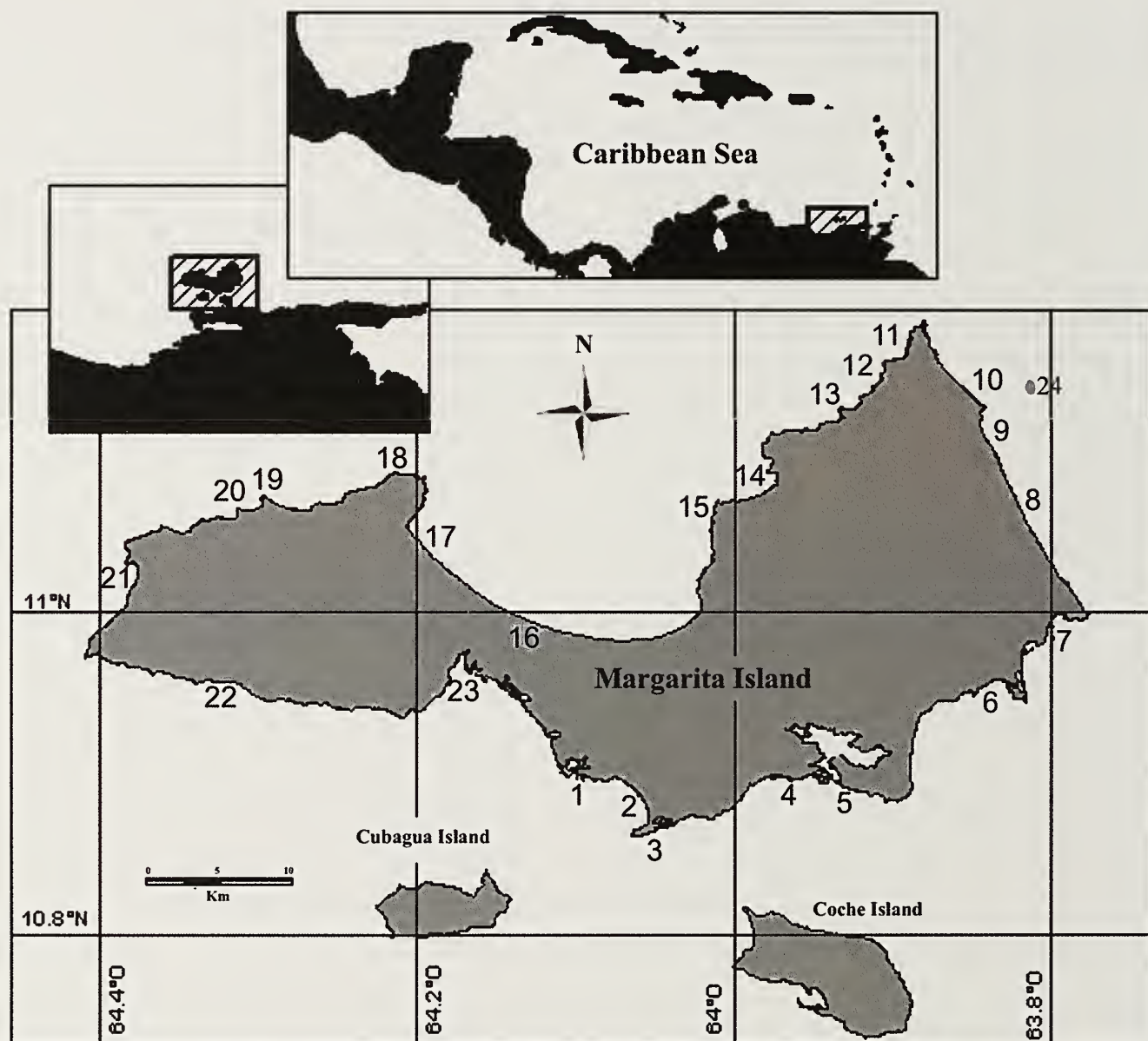
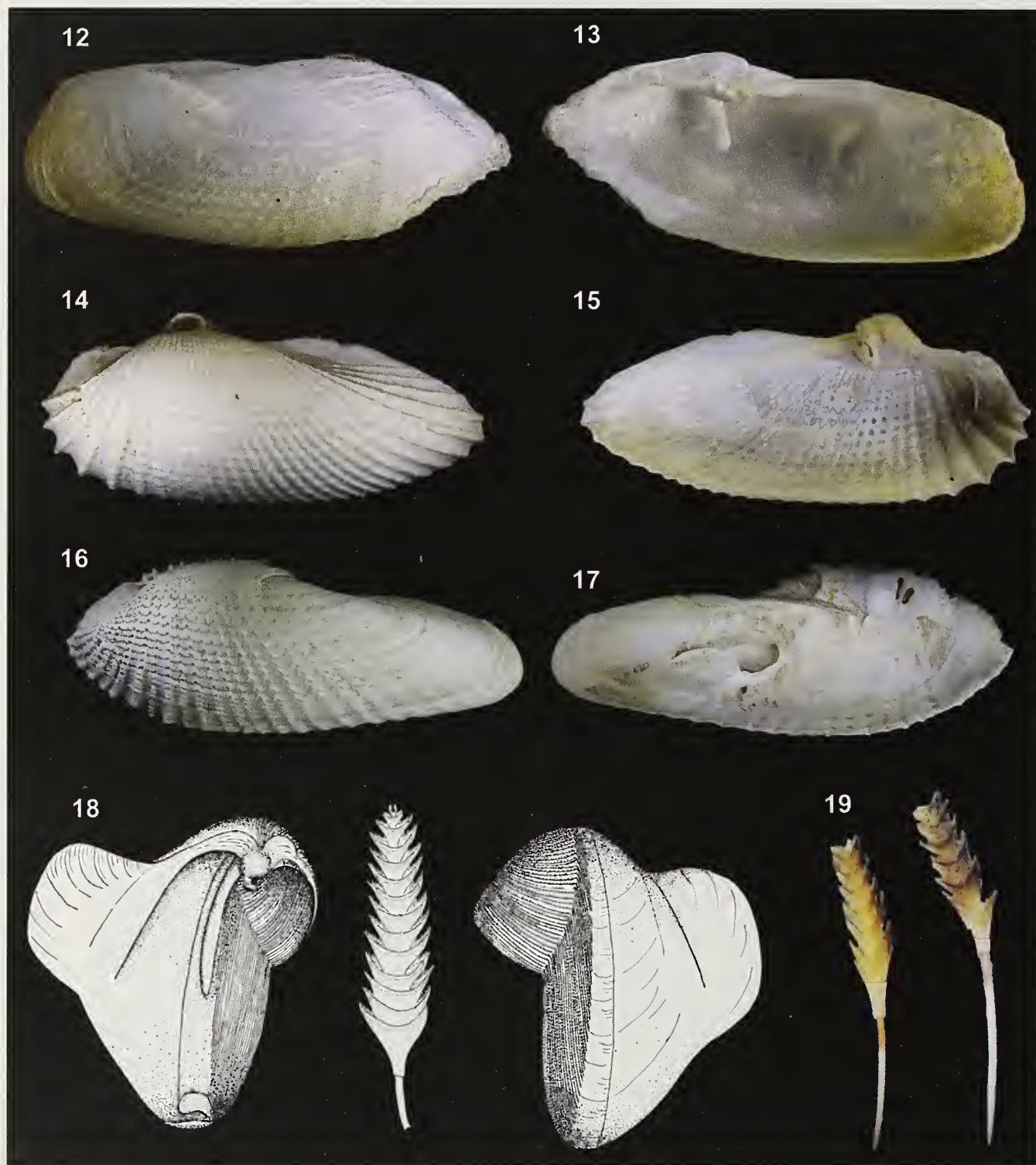


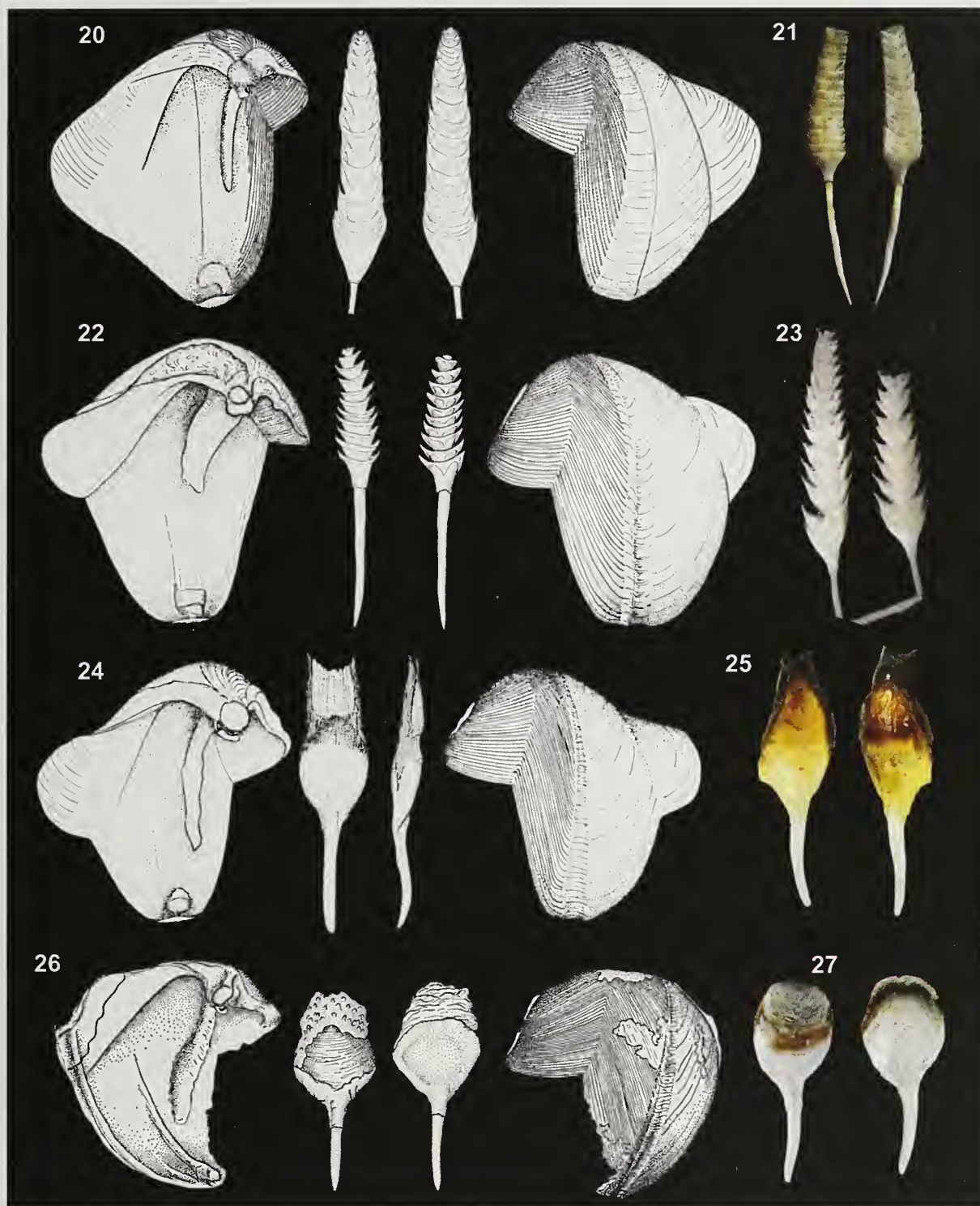
Figure 1. Sampling stations of endolithic bivalve mollusks along Isla Margarita and Los Frailes archipelago.



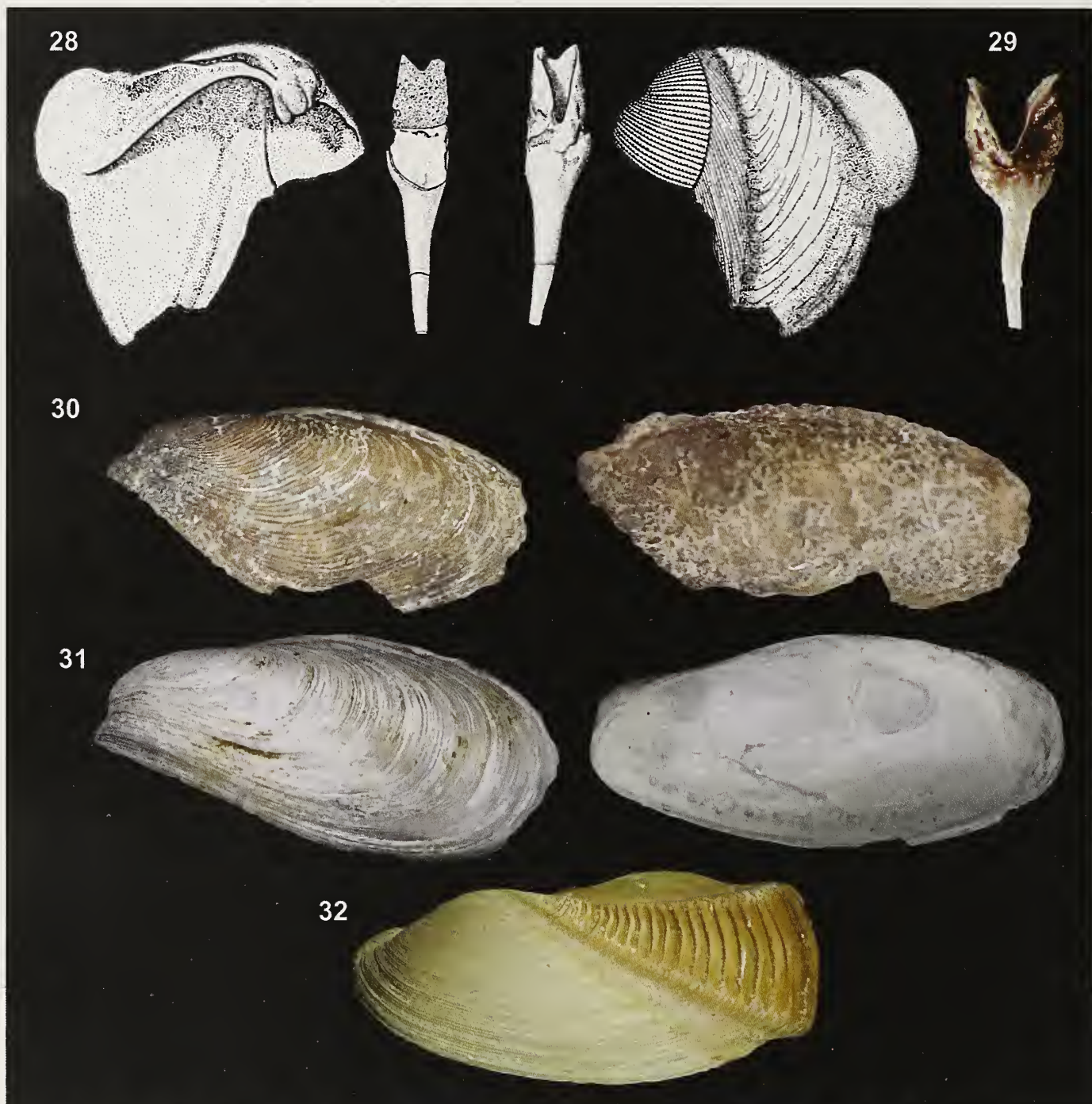
Figures 2-11. 2. Lateral view of left valve of *Leiosolenus aristatus*, MOBR-M-3190, Playa Parguito, length = 29.9 mm. 3. Lateral view of left valve of *Leiosolenus bisulcatus*, MOBR-M-3184, Punta de Piedras, El Atolladar, length = 27.0 mm. 4. Lateral view of left valve of *Lithophaga antillarum* (anterior portion of valve missing), MOBR-M-3171, El Guamache, Varadero, length = 38.2 mm. 5. Lateral view of right valve of *Gregariella coralliophaga*, MOBR-M-0157, Pampatar, length = 11.1 mm. 6. Lateral view of *Choristodon robustus*, MOBR-M-3178, El Maguey, length = 17.2 mm. 7, 8. Lateral exterior and interior views of *Martesia cuneiformis*, MOBR-M-3977, Porlamar, Laguna El Morro, length = 6 to 7 mm. 9, 10. Lateral and dorsal view of *Martesia fragilis*, MOBR-M-3934, Boca de Pozo, length = 10.2 mm. 11. Lateral view of *Martesia striata*, MOBR-M-1238, Punta de Piedras, length = 26.9 mm.



Figures 12-19. 12, 13. Lateral views of interior and exterior of *Barnea truncata*, MOBR-M-3177, Playa La Restinga, El Saco, length = 51.4 mm. 14, 15. Lateral views of exterior and interior of *Cyrtopleura costata*, MOBR-M-1067, La Restinga, length = 64.2 mm. 16, 17. Lateral views of exterior and interior of *Pholas campechiensis*, MOBR-M-3176, La Restinga, Playa El Saco, length = 99.7 mm. 18-19. *Bankia destructa*: 18, lateral views of interior and exterior, pallets, MCZ 123303, holotype, length = 4 mm (after Clench & Turner, 1946); 19, pallets, MOBR-M-3938, Punta de Piedras, length = 3.0 mm.



Figures 20-25. 20-21. *Bankia gouldi*: 20, lateral views of interior and exterior, pallets, MCZ unnumbered, shell length = 7 mm (after Clench & Turner, 1946); 21, pallets, MOBR-M-3939, Punta de Piedras, length = 4.4 mm. 22-23. *Bankia carinata*: 22, lateral views of interior and exterior, pallets, lectotype of *Teredo stuchburyi*, BMNH 20050252, shell length = 4 mm (after Turner, 1946); 23, pallets, MOBR-M-3983, Punta de Piedras. 24-25. *Lyrodus pedicellatus*: 24, lateral views of interior and exterior, pallets, length = 4 mm (after Turner, 1966); 25, pallets, MOBR-M-3929, La Isleta, Las Marites. 26-27. *Spathoteredo spatha*: 26, lateral views of interior and exterior, pallets, lectotype, USNM 194272, shell length = 7 mm (after Turner, 1966); 27, pallets, MOBR-M-3983, Punta de Piedras.



Figures 28-32. 28-29. *Teredo furcifera*, 28, lateral views of interior and exterior, pallets, holotype, Museum für Naturkunde unnumbered, shell length = 7 mm (after Turner, 1966); 29. pallets, MOBR-M- 3930, La Isleta, Las Marites. 30. *Gastrochaena ovata*, lateral views of exterior and interior, MOBR-M-3928, Playa El Tunal, length = 12.5 mm. 31. *Lamychaena hians*, lateral views of exterior and interior, MOBR-M-3172, Boca Chica, length = 15.0 mm. 32. *Spengleria rostrata* lateral view of exterior, MOBR-M-3170, Los Frailes Archipelago, Punta Cachipo, length = 28.6 mm.